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Beck (1968b) supports this view and regards the unilacunar one-trace node as the primitive condition in the Coniferales.

My observations reveal that mature nodes of Dillenia (FIG. 8), Didesmandra, and Schumacheria (FIG. 7) are exclusively multilacunar.¹ The numerous leaf traces are associated with a corresponding number of parenchymatous gaps in the cauline stele. The number of traces in Schumacheria and Didesmandra was found to be stable at nine and seventeen respectively. The number in Dillenia, however, varies from as few as seven (D. pulchella) to as high as twenty-seven (D. suffruticosa). Variability is also evident within a single species, the number of traces apparently reflecting the age and size of the node. The manner in which bundles depart the stele was found generally to be correlated with the presence or absence of sheathing leaf bases. If the petiole does not sheath the stem, all traces tend to depart simultaneously. If the leaves are amplexicaul, the median trace passes out initially, with laterals departing in succession at higher levels. The leaves examined of the semi-herbaceous, rhizomatous genus Acrotrema were supplied by three traces; i.e., the node was trilacunar (FIG. 4). The median trace departs first with the resulting gap remaining open above the level at which the two lateral gaps close. Large-leaved species (e.g., A. arnottianum) should be studied when available to determine to what extent leaf size affects the nodal pattern in this extremely variable genus.

In contrast to the information presented by Ozenda (1949), all hibbertias are not uniformally trilacunar. Numerous species with reduced, needle-like leaves possess unilacunar nodes (FIG. 2). In these cases, the primary stele is composed of a continuous cylinder of vascular tissue with no discrete bundles discernible. At the unilacunar node, a single trace passes directly into the leaf. All broad-leaved hibbertias from New Caledonia and Fiji are trilacunar. Leaf size is not always indicative of nodal patterns, however. Trilacunar *Hibbertia huegelli* (FIG. 45) and *H. monogyna* (FIG. 46), for example, possess smaller leaves than *H. nitida* (FIG. 47) which is unilacunar. The most reduced leaves in the family are encountered in the genus *Pachynema*. The small, scale-like, lateral appendages were found to be vascularized by a single prominent trace with a well defined gap in the stele. From the flattened stem of *P. dilatatum*, leaves may be secondarily supplied by weak cauline traces (FIG. 34).

The New World genera Curatella, Davilla (FIG. 6), and Doliocarpus are mostly pentalacunar; but seven-trace nodes occur in Davilla aspera, and Doliocarpus major is trilacunar. Trilacunar, three-trace nodes are also uniform throughout the genus Tetracera where special effort was made to examine representative species from the Old and New World tropics. In Tetracera, three bundles are associated with three widely separated

¹The report by Benzing (1967a) of unilacunar one-trace nodes in the mature stems of *Dillenia indica* is in error. I have personally examined the sections used in this study and conclude that they were not taken from any member of the Dilleniaceae.

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gaps (FIG. 3). The lateral bundles arc up and through the cortex where they enter the petiole. This contrasts with the condition in the trilacunar hibbertias with sheathing leaf bases, where the laterals enter the leaf directly from the stele (FIG. 5).

The seedling anatomy of Dillenia indica, Tetracera indica, Hibbertia dentata, and H. scandens was examined. The cotyledonary nodes in the first two species are of the 2:1 type, viz., two traces departing from a single gap (FIGS. 1, 40). My observation of the 2:1 cotyledonary nodal pattern in Dillenia indica once again contradicts the information presented by Ozenda (1949) who illustrated a single cotyledonary trace. Particular attention was paid to the double traces at subnodal levels and in all instances they originated from independent parts of the stele. In Dillenia indica, a species with multilacunar nodes in the mature stem, the first formed seedling leaves possess a trilacunar node (FIG. 41). Numerous examples can be found in other dicotyledonous families of a similar progression, as in Magnoliaceae, Degeneriaceae, etc. The cotyledonary node of Hibbertia dentata and H. scandens differs by being of the unilacunar one-trace type (FIG. 12). No evidence of doubleness could be observed in the single, broad strand of vascular tissue which passes into the cotyledon. The occurrence of a 1:1 cotyledonary node in Hibbertia is of particular interest, since it is a genus with trilacunar mature nodes, and is generally considered to be more primitive in its characters than either Dillenia or Tetracera. The question again arises whether an even or odd number of nodal traces represents the primitive condition. A thorough study of the cotyledonary node in other Dilleniaceae would be worthy of careful attention. It is perhaps significant, that more than one case was observed among the seedling and mature nodes of Dillenia where an even number of traces prevailed. This condition resulted from suppression of one of the lateral bundles with the result that an even number of traces departed the stele. Although this might be dismissed as abnormal, the fact that it was observed more than once indicates that it may be of some significance. Although the majority of plant families exhibit a combination of unilacunar and trilacunar, or trilacunar and multilacunar nodes, it is relatively uncommon for a single family to possess all three types (Bailey & Nast, 1944). The Dilleniaceae are, therefore, unusual in possessing four patterns: unilacunar two-trace, unilacunar one-trace, trilacunar, and multilacunar. Bailey (1956) points out that transitions from trilacunar to unilacunar nodes may occur as the result of anatomical specialization in response to the environment. The reduction of leaf size in Hibbertia is such an adaptation. Thus, the mature foliage nodes in Dilleniaceae (sensu stricto) demonstrate two distinct trends of specialization: (1) secondary reduction and elimination of the lateral strands of the trilacunar nodes; and (2) amplification of the trilacunar node by the addition of laterals. Bailey and Howard (1941) note that trends of specialization in nodal anatomy are not infrequently correlated with specializations elsewhere in the plant (e.g., wood). No such direct correlations were noted in the dil-

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lenias. In fact, those genera having the least advanced wood generally possess the more highly evolved nodes.

It is not possible to construct relationships within the family solely on the basis of nodal structure due to the presence of a similar anatomy in both Old and New World genera. Likewise, nodal anatomy is of limited value in determining relationships beyond the family. When the nodes of putatively related families are compared, it is evident that they are all essentially tri- or multilacunar. There is, accordingly, no basis for accepting or rejecting alliances from this information alone.

A significant exception to the above generalizations is found in the Theaceae where the node is uniformly characterized by a broad trace which departs from a single gap. Keng (1962) agreed with Canright (1955) in considering this pattern to be the result of phylogenetic fusion of several separate traces. If Canright's (*loc. cit.*) suggested trends of nodal specialization are accepted, it leads one to the conclusion that the nodal anatomy in the two families represents the culmination of distinct lines of evolution. Therefore, although the wood and pollen of these groups is similar (Dickison, 1967a, b), nodal anatomy suggests they may in fact be only distantly related. A similar conclusion might be reached regarding the predominantly unilacunar, one-trace nodes of Ericaceae; however, the report by Philipson and Philipson (1968) of trilacunar nodes in *Rhododendron* gives cause for re-evaluation.

PETIOLE VASCULARIZATION

An attempt to define the range of variability in petiolar anatomy of Dilleniaceae disclosed the following major patterns:

Species with Unilacunar Nodes (1:1).

 A single, slender, unbranched trace enters the lamina: numerous hibbertias (FIG. 27).

Species with Trilacunar Nodes (3:3).

- (1) Traces fuse and form a flattened arc: Hibbertia quadricolor.
- (2) Traces fuse and form "V" shaped arc: Hibbertia coriacea (FIG. 17).
- (3) Traces fuse and form cylindrical, flattened, or concave vascular ring, either confluent or slightly dissected: Doliocarpus major; D. olivaceus;² Hibbertia dealbata; H. oubatchensis; H. patula (FIG. 14); H. trachyphylla; Tetracera akara; T. arborescens; T. daemeliana (FIG. 16); T. korthalsii; T. macrophylla; T. ovalifolia; T. portobellensis; T. scandens; T. volubilis.
 (4) Traces form a closed cylindrical ring with one or more medullary bundles produced by invagination: Hibbertia lucida (FIG. 13).
 (5) Traces form an abaxial arc of fused or dissected collateral bundles with a separate adaxial trace derived from the inrolling and/or division of the lateral bundles. The adaxial trace may be lost in the lamina: Acrotrema

² Nodes were not examined.

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sp.; A. bullatum; A. gardneri; A. lanceolatum; A. uniflorum; A. walkeri; Hibbertia banksii; H. pancheri; H. wagapii; Tetracera boiviniana; T. masuiana.

(6) Traces form an abaxial arc of fused or dissected collateral bundles with a separate adaxial trace derived from division of the median bundle. The adaxial trace may be lost in the lamina: *Hibbertia scandens*; *Tetracera indica*.

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Species with Multilacunar Nodes (five to many traces from an equal number of gaps).

- Traces remain free forming a ring of widely dissected collateral bundles (bundles are often of unequal sizes): Acrotrema costatum; ² Didesmandra (FIG. 15); Dillenia excelsa; D. luzoniensis; Schumacheria angustifolia.
- (2) Traces fuse to form confluent or only slightly dissected ring, often "U" or "V" shaped in outline: Davilla (FIG. 22); Dillenia bolsteri (FIG. 19); D. eximia; D. indica; D. ovata; D. pentagyna; D. salomonensis; D. suf-fruticosa; D. turbinata.
- (3) Traces fuse to form confluent or only slightly dissected ring with an arc (rarely superimposed) of fused or dissected medullary bundles: Curatella americana (FIGS. 10A,B,C); Dillenia alata; D. beccariana (FIG. 20); D. castaneifolia (FIG. 18); D. megalantha; D. papuana; D. philippinensis; D. reifferscheidia.
- (4) Traces form an abaxial arc of fused or dissected collateral bundles with an adaxial enclosed siphonostele. The adaxial ring may subsequently open laterally or invaginate to produce additional free bundles: Doliocarpus

coriaceus; D. dentatus; D. guianensis (FIG. 21); D. rolandri.

It is evident that petiole vascularization in Dilleniaceae is quite diverse both between and within genera. In the present study, subtle deviations in vascularization pattern, the general outline of the vascular cylinder, and small, adaxial, subsidiary wing traces were ascribed little importance. Despite acknowledged incompleteness, I feel the descriptions outlined above will prove useful in future comparative studies relating to the family. It should be emphasized, that the descriptions presented are not based entirely upon observations from a single "characteristic" region. Wherever possible, sections were examined throughout the petiole and midrib as suggested by Howard (1962). The importance of determining the entire sequence of petiole vascularization is well exemplified in study of the Dilleniaceae. Not only are there significant fluctuations within a single petiole, but patterns which appear superficially similar between genera

can be shown to have different origins. An example of the latter situation is illustrated by *Hibbertia scandens* and the Ceylonese acrotremas, both of which possess petioles with an abaxial arc and adaxial strand of vascular tissue. However, the adaxial bundle is derived from the median trace in *H. scandens* (FIGS. 11A,B,C), whereas it originates from the lateral nodal bundles in *Acrotrema* (FIGS. 9A,B,C,D). The diversity present at the species level indicates that the petiole may be of taxonomic significance in the family. In the New World genus *Do*-

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liocarpus, D. major and D. olivaceus are distinguished by their pubescent ovaries and fruits. An absence of medullary bundles in the petiole was also found to separate these taxa readily from all other species examined in the genus. Hunter (1966) considers Doliocarpus rolandri Gmel. to be a synonym of D. major Gmel. I have studied a collection from Brazil cited as D. rolandri (Pires & Cavalcante 52254, US) and found the petiole to possess medullary bundles, a character which is not encountered in D. major. A re-examination of this genus taxonomically might yield additional basis for separation of the species. Other specific variation is found in Acrotrema (where A. costatum, from Thailand and Malaya, is quite distinct from the Ceylonese species), Hibbertia, and Dillenia, though much more material must be studied before the true value of these data can be realized. Petiole structure cannot be used to separate the Dilleniaceae into subfamilies or tribes. Moreover, there is little or no correlation between petiole vascularization and nodal anatomy. When considered as a whole, the vascular pattern in species with trilacunar nodes cannot be considered more primitive than that in species with multilacunar nodes. In plants with multilacunar nodes, petioles with widely dissected cylinders tend to be correlated with slender venation lacking massive bundle sheathing, which I consider primitive. With intensification of leaf venation and bundle sheathing, the complexity of the petiolar anatomy also increases. I believe, therefore, that unfused bundles represent the primitive condition in multilacunar dillenias. Subsequent evolutionary progression has produced fusion of traces and the formation of more complex medullary bundle patterns. These specializations have apparently occurred more than once, since the same apparent trends are also evident in species with trilacunar nodes. These ideas of nodal and petiolar evolution in Dilleniaceae do not agree with the conclusions of Decker (1967) who worked on the Luxemburgieae (Ochnaceae). Within the Luxemburgieae, Decker considers the multilacunar node more primitive than the trilacunar, and petioles with numerous, unfused bundles (some of which may be medullary), more primitive than petioles with fused traces devoid of medullary bundles. In view of the frequent derivation of the Ochnaceae from the Dilleniaceae, such contrasting opinions are of special interest.

A foliar character of debatable morphological derivation is the presence of petiolar wings in some Old World dilleniaceous species. Hoogland (1952) attaches taxonomic importance to the presence of completely amplexicaul petiolar wings in certain species of *Dillenia*. Morphologically, these wings are frequently considered to be stipules. Hoogland (*loc. cit.*) does not accept this interpretation for the following reasons: (1) there is often no sharp distinction between the petiolar wings and lamina, (2) stipules of the usual morphological type do not occur in the dillenias, (3) in caducous wings, separation from the petiole begins from the base of the petiole and not from the apex as one would expect, and (4) Ozenda (1949) describes the wings as being weakly vascularized in contrast to the situation

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in the Magnoliaceae where the stipules receive a separate trace from the cauline stele.

I have found vascularization of the wings in Dillenia to vary from weak (e.g., D. albiflos) to rather strong (e.g., D. philippinensis; D. suffruticosa). In the latter case the venation is highly reticulate. In either situation the wings are never supplied by independent traces from the cauline stele. Although I do not have any original interpretation for these structures, they do not appear comparable to true stipules.

VASCULARIZATION OF THE LAMINA

Major Venation. Although the prevailing type of major foliar venation in the Dilleniaceae is pinnate, with the secondary veins proceeding to the margin of the blade, wide variation in leaf size, shape, and vascularization is encountered in the genus Hibbertia. A study of leaf vasculature in this genus showed that three basic venation patterns can be recognized: (1) pinnate leaves in which the numerous, strong, parallel, lateral veins extend diagonally outward from the midvein toward the margin of the lamina where they are interconnected by curved peripheral venation (FIG. 43); (2) pinnate leaves in which the principal lateral veins are fewer in number, irregular in their occurrence, more tenuous, and tend to sweep upward upon departure from the midvein (FIGS. 42, 44); and (3), a pattern where two or more strong, terminal, lateral veins reflex back after departure from the midrib to terminate, often very massively, at the leaf base. A varying number of prominent lateral veins may connect the midrib with the reflexed lateral (FIG. 49). This specialized venation pattern is exclusively associated with those hibbertias with reduced, needle-like leaves. The physiological significance of this type of vasculature is not clear. Concomitant in Hibbertia with a general trend toward reduction in leaf size as a response to xerophytic conditions, is a trend in reduction of leaf vascularization. Theoretically, this specialization commences with the progressive loss of the basal lateral veins connecting the midrib and reflexed laterals (FIGS. 47, 48) so as eventually to reach a situation where the reflexed veins are without major interconnecting venation (FIG. 49). The ultimate reduction is represented in H. fasciculata where only a small number of very weak reflexed apical veins are present; the lower one-half of the leaf is entirely devoid of venation, excepting the midvein (FIG. 50). Cotyledons of Dillenia indica, Tetracera indica, and Hibbertia dentata differ in shape from ovate, to oblong-elliptical, to linear-lanceolate, but all veins (FIG. 40). Another feature of cotyledonary vasculature is the

exhibit fundamentally similar venation. The vasculature is characterized by the presence of strongly accentuated, arcuate basal lateral veins which terminate in, or near, the cotyledon apex. Several less prominent veins diverge from the midrib to connect with the strongly ascending basal "feathery" termination of the midvein and arcuate laterals. Feathery termination of the midrib was also observed in the mature leaves of the family. JOURNAL OF THE ARNOLD ARBORETUM [vol. 50 The first-formed seedling leaves of *Dillenia indica*, with their strong, parallel, pinnate veins and serrate margins are sharply distinguished from the cotyledons (FIG. 41).

Minor Venation. In addition to noteworthy features of major venation, the pattern and diameter of the minor veins, in association with bundle sheathing, is often of diagnostic and perhaps of taxonomic significance in the Dilleniaceae.

The occurrence of bundle sheaths around the veins is almost a universal feature of dilleniaceous leaves. Sheathing is noticeably absent only in some hibbertias and Acrotrema. When present, the sheath cells are either unlignified and parenchymatous in nature, or lignified, pitted, sclerenchymatous elements. Parenchymatous sheaths typically surround both the major veins and terminal veinlets. These sheaths usually consist of cells elongated parallel to the vascular bundles; however, occasionally they become considerably lobed and oriented at right angles to the veins (FIG. 33). Sclerotized bundle sheathing is recognized by the presence of lignified, extensively pitted cells. When sclerenchyma occurs, it may form massive sheaths over the veins and veinlets as in Hibbertia (FIG. 30), Tetracera (FIG. 32), and some species of Doliocarpus. The formation of sclerified bundle sheaths enclosing the terminal tracheids is an uncommon feature in dicotyledonous leaves (Esau, 1965). Of more frequent occurrence in the family is sclerenchyma around the major veins, but with veinlets devoid of sheathing or possessing only an incomplete sheath. The most striking pattern is seen in Hibbertia banksii where the mature leaves exhibit an interrupted sclerenchymatous sheath (FIG. 29). Parenchymatous sheath cells were observed in Curatella (FIG. 31) and all species of Dillenia (FIG. 23), except D. philippinensis and D. reifferscheidia where pitted elements are found. Also, the presence of lobed parenchymatous sheathing around the terminal veinlets in Doliocarpus dentatus (FIG. 33) and D. rolandri readily distinguishes them from all other species of the genus. The variation present in Doliocarpus in the node, petiole, and minor venation warrants further study. Distinctions can also be made between genera and species on the basis of the diameter of veins and veinlets. Very slender venation is present in Acrotrema, Didesmandra (FIG. 26), Schumacheria, and some hibbertias (H. scandens, H. dentata, H. tetrandra, etc.). Associated with slender vascularization is weak bundle sheathing or its complete absence. Only in Hibbertia is massive venation sometimes devoid of sheathing (FIG. 28). There appears, nevertheless, to be in the family a rather distinct trend toward increased vein size accompanied by intensification of the amount of vein sheathing.

A restricted trend was observed in *Dillenia* toward the formation of vein islets devoid of free vein endings. It is possible to trace this progression from species with slender veins and numerous free vein endings (e.g.

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D. salomonensis and FIG. 23) through species with an intermediate pattern (e.g. D. quercifolia, D. ovalifolia, D. nalagi) to a pattern illustrated by D. papuana (FIG. 24) where free vein endings are scarce. The terminal condition in this sequence is seen in the massive, closed venation of D. schlechteri (FIG. 25).

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A taxonomic correlation of minor venation patterns in Dillenia is illustrated by similar closed venation types occurring in D. papuana, D. cyclopensis, and D. schlechteri, all of which are considered closely related by Hoogland (1959) on the basis of floral structure. The only other species which were observed to possess comparable vasculature were D. beccariana, and D. turbinata. On the basis of leaf venation, I was not able to segregate Wormia as a distinct genus from Dillenia. The leaves of the Dilleniaceae appear to display a rather distinct phylogenetic trend of specialization toward more massive vascularization, accompanied by an increase in bundle sheathing. The same fundamental trends have also been described for the Winteraceae (Bailey & Nast, 1944). When the venation pattern, size, type, and degree of bundle sheathing, as well as petiole vasculature, are considered together, they offer excellent diagnostic leaf characters at the family, genus, and in some instances, species level. Additional material in all stages of maturity will have to be examined to understand fully the taxonomic significance of this information.

TERMINAL IDIOBLASTS

The occurrence of specialized terminal-veinlet elements in several widely diverse dicotyledonous families has been well established. In a recent review of the literature, Tucker (1964) describes their presence in the Magnoliaceae. The occurrence of terminal idioblasts is now reported for the first time in the Dilleniaceae.

Specialized terminal cells were observed only in relatively few species of Hibbertia. The diversity in vein endings is thus in accordance with variation in leaf shape and venation. The terminal cells are all of the basic tracheoid type (see Foster, 1956). Employing the classification of Tucker (loc. cit.), one can recognize tracheoidal elements, viz. scalariform or scalariform-reticulate pitted cells, and dilated tracheids. Leaves of H. scandens (cult. K, s.n.) and H. dentata (cult. K, s.n.) were found to contain terminal elements which closely resemble tracheary cells in general morphology. The elements in H. dentata (FIG. 36) tend to occur singly and have exclusively scalariform pitting whereas the idioblasts of H. scandens (FIG. 35) often occur in clusters where they assume more irregular shapes and have reticulate pitting. The terminal elements of Hibbertia pachyrhiza (C. L. Wilson 861, FIG. 38), although of the basic tracheoid type, differ considerably in their morphology. The latter cells are thick-walled, pitted to a much less degree, and are characteristically spherical in outline. In comparison with surrounding parenchyma these elements are significantly larger (75-140 μ in

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Terminal elements in Hibbertia huegelli (C. L. Wilson 777), H. monogyna (Maiden s.n.), H. elata (Ingram 19852), H. billardieri (Clemens 42584a), and H. linearis (White 8580) tend to be intermediate between the elongated tracheoid element and the spherical one (Fig. 37).

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Dilated tracheids were found in Hibbertia scandens (FIG. 39), H. dentata, H. nymphaea (Morrison s.n., A), and H. amplexicaulis (Pritzel 531). In H. scandens and H. dentata they were often in the same leaf with tracheoidal elements, and several veins were noted where the two types were present at the same vein endings. Generally, however, dilated tracheids seem to occur rather sparsely throughout the leaf and are not present at every vein terminus. The taxonomic usefulness of terminal idioblasts in the Dilleniaceae appears limited in view of their rather infrequent occurrence. Phylogenetically it is of interest that the most diverse vein endings are found in Hibbertia, which on the basis of other criteria, is considered rather primitive. A similar situation has been reported in the Magnoliaceae (Tucker, loc. cit.). The full phylogenetic value of terminal idioblasts still remains to be developed; however, the trend toward the formation of specialized terminal cells appears to be a distinct one, subsequently leading toward the reduction in size of the elements and in the amount of pitting on the wall surface.

SUMMARY

A comprehensive study of nodal and leaf vascularization in Dilleniaceae has led to the following fundamental conclusions:

- (1) The mature foliar nodes of Dilleniaceae (sensu stricto) are unilacunar one-trace, trilacunar, and multilacunar. The unilacunar and multilacunar patterns are both derived from the trilacunar condition. The cotyledonary node is unilacunar two-trace or unilacunar one-trace. Evidence from nodal anatomy appears to discredit a close relationship between the Dilleniaceae and Theaceae.
- The petiolar anatomy of the family shows considerable diversity. Descriptions of major venation patterns reveal that, in general, vascular cylinders composed of widely dissected bundles are more primitive than petioles with fused bundles and more complex medullary traces.
 The vascularization of the lamina displays fundamental phylogenetic trends of specialization in both major and minor venation. Bundle sheath cells are either parenchymatous or sclerenchymatous and may enclose the terminal tracheids. Slender venation patterns lacking bundle sheathing are less specialized than coarser-veined leaves with massive bundle sheathing.
 When considered together, nodal anatomy and foliar vasculature are of excellent diagnostic value and frequently of taxonomic and phylogenetic significance in the Dilleniaceae.

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(5) The presence of specialized terminal idioblasts in the leaves of *Hibbertia* is a character of which the importance is yet to be determined.

MATERIAL EXAMINED

Acrotrema sp. Ceylon: Thwaites CP3899 (US). A. bullatum Thw. Ceylon: Thwaites CP239 (US). A. costatum Jack. Thailand: Smitinand 2999 (US). A. gardneri Thw. Ceylon: Thwaites CP253 (US). A. lanceolatum Hook. Ceylon: Thwaites CP2660 (US). A. uniflorum Hook. Ceylon: Thwaites CP1014 (US). A. walkeri Wight. Ceylon: Thwaites CP694 (US).

Curatella americana L. Brazil: Irwin 5470 (NY); Nicaragua: Van der Sluijs s.n. (preserved material).

Davilla aspera (Aubl.) Benoist. Trinidad: Howard 10502 (GH); Brazil: N.T. Silva 16. D. multiflora (DC). St. Hil. Panama: Dodge & Allen 17360 (мо). D. rugosa Poir. Brazil: A. de Mattos Filho s.n. (preserved material). Davilla sp. Brazil: Irwin 5570 (NY).

Didesmandra aspera Stapf. Sarawak: Burtt & Woods B.2540 (E); S.18297 (SAR); Native collector (SAR) s.n. (preserved material).

Dillenia alata (R.Br. ex DC.) Mart. New Guinea: P. van Royen 4677 (A, US). D. albiflos (Ridl.) Hoogl. Malaya: Corner SING F 29369 (A). D. beccariana Martelli. Sarawak: SAR 16272 (A). D. biflora (A. Gray) Martelli ex Dur. & Jacks. Fiji: Gillespie 2182 (GH); A. C. Smith 8762 (US). D. bolsteri Merr. Philippines: Wenzel 3112 (GH). D. castaneifolia (Miq.) Martelli ex Dur. & Jacks. New Guinea: Womersley NGF 3768 (A). D. cyclopensis Hoogl. New Guinea: van Royen & Sleumer 5812 (A). D. excelsa (Jack) Gilg. North Borneo: Ramos 1379 (A). D. eximia Miq. Borneo: NIFS bb 16830 (A). D. indica L. Australia: Cult. BRI s.n. (preserved material); India: Sastri s.n. (preserved material); Cult. E C4388. D. luzoniensis (Vidal) Martelli ex Dur. & Jacks. Philippines: J. V. Pancho s.n. (preserved material). D. megalantha Merr. Philippines: Quezon. M. Q. Lagrimas s.n. (preserved material). D. monantha Merr. Philippines: Herre 1010 (A). D. montana Diels. New Guinea: Hoogland & Pullen 6265 (A). D. nalagi Hoogl. Papua: Hoogland & Taylor 3438 (A). D. ochreata (Miq.) Teysm. & Binn. ex Martelli. Celebes: NIFS bb 18085 (A). D. ovalifolia Hoogl. New Guinea: van Royen 3012 (A). D. ovata Wall. ex Hook.f. & Thoms. Indo-China: Squires 320 (A); Cult. SING s.n. (preserved material). D. papuana Martelli. Papua: Womersley NGF 3926 (A); NGF s.n. (preserved material). D. pentagyna Roxb. India: Ellis 23815 (мн). D. philippinensis Rolfe. Philippines: Makiling. M. Q. Lagrimas s.n. (preserved material). D. pulchella (Jack) Gilg. Singapore: Cult. SING s.n. (preserved material). D. quercifolia (White & Francis ex Lane-Poole) Hoogl. Papua: Hoogland 3286 (A). D. reifferscheidia Villar. Philippines: Quezon. Lagrimas s.n. (preserved material). D. reticulata King. Sarawak: SAR 16655 (A). D. salomonensis (White) Hoogl. Solomon Islands: Walker & White 145 (A). D. schlechteri Diels. New Guinea: Womersley & Millar NGF 7000 (A). D. suffruticosa (Griff.) Martelli. Singapore: Cult. SING S.N. (preserved material); Canright 978 (ASU). D. turbinata Fin. & Gagnep. Hainan: How 72058 (A).

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Doliocarpus coriaceus (Mart. & Zucc.) Gilg. British Honduras: Gentle 2892 (US); Colombia: Cuatrecasas 16556 (US). D. dentatus (Aubl.) Standl. Bolivia: Krukoff 396 JOURNAL OF THE ARNOLD ARBORETUM [VOL. 50

10088 (UC). D. guianensis (Aubl.) Gilg. Surinam: UC 947180. D. lasiogyne Benoist. Brazil: Klein 1.281 (US). D. major Gmel. Panama: von Wedel 2860 (мо); I. M. Johnston 1694 (мо). D. olivaceus Sprague & Williams ex Standl. Panama: Stern et al. 11 (US). D. rolandri Gmel. Brazil: Pirés & Cavalcante 52254 (US).

Hibbertia acicularis (Labill.) F. Muell. Australia: Queensland. Clemens 43622 (A); C. T. White 9466 (A). H. altigena Schlechter. New Caledonia: H. S. McKee 3709 (A). H. amplexicaulis Steud. Australia: Pritzel 531 (A). H. aspera DC. Australia: New South Wales. Constable 42837 (A). H. aurea Steud. Aus-

tralia: C. L. Wilson 843 (US). H. australis Wakefield. Australia: Aston 359 (A). H. banksii Benth. Papua: L. J. Brass 8431 (A). H. baudouinii Brongn. & Gris. New Caledonia: Baumann-Bodenheim 11203 (A). H. bracteata (R.Br.) Benth. Australia: New South Wales, C. T. White 5012 (A). H. billardieri F. Muell. Australia: Queensland. Clemens 42584a (us). H. brongniartii Gilg. New Caledonia: Thorne 28580 (RSA). H. cistiflora Wakefield. Australia: New South Wales. Helms 1290 (A). H. cistifolia R.Br. Australia: Specht 843 (US). H. coriacea (Pers.) Baill. Madagascar: Humbert 5866 (US). H. crenata Andr. Australia: C. L. Wilson 851 (US). H. cuneiformis (Labill.) Gilg. Australia: Cult. K, s.n. (preserved material); E. H. Wilson 297 (US). H. dealbata Benth. Australia: Specht 844 (A). H. dentata R.Br. Cult. к, s.n. (preserved material). H. deplancheana Bur. ex Guillaum. New Caledonia: Thorne 28232 (GH). H. depressa Steud. Australia: Royce 5760 (US). H. ebracteata Bur. ex Guillaum. New Caledonia: H. S. McKee 3697 (A). H. elata Maiden & Betche. Australia: New South Wales. Ingram 19852 (US). H. exutiacies Wakefield. Australia: Eichler 17965 (AD). H. fasciculata R.Br. ex DC. Australia: Aston 387 (A). H. furfuracea Benth. Australia: C. T. White 5382 (A). H. gilgiana Diels. Australia: C. L. Wilson 856 (US). H. glaberrima F. Muell. Australia: Perry 5379 (US). H. gracilipes Benth. Australia: Royce 5792 (US). H. huegelli F. Muell. Australia: C. L. Wilson 777 (US). H. hypericoides (DC.) Benth. Australia: E. H. Wilson 454 (A). H. lasiopus Benth. Australia: C. L. Wilson 781 (US). H. linearis R.Br. ex DC. Australia: Queensland. C. T. White 8580 (A); Hoogland 7747 (CANB). H. lucens Brongn. & Gris. Fiji: A. C. Smith 6494 (A); A. C. Smith 1877 (GH). H. lucida Schlechter ex Guillaum. New Caledonia: C. T. White 2210 (A). H. melhanioides F. Muell. Australia: C. L. Wilson 740 (US). H. microphylla Steud. Australia: C. T. White 5317 (A). H. miniata Gard. Australia: C. L. Wilson 782 (US). H. monogyna R.Br. ex DC. Australia: New South Wales. J. H. Maiden s.n. (GH). H. montana Steud. Australia: C. L. Wilson 839 (US). H. mucronata (Turcz.) Benth. Australia: C. L. Wilson 792 (US). H. nana Däniker. New Caledonia: Baumann-Bodenheim 15358 (A). H. nitida (R.Br.) F. Muell. Australia: Fl. Novae Holl. 141 (GH). H. nymphaea Diels. Australia: Morrison s.n. (A). H. obtusifolia DC. Australia: New South Wales. Pullen 3882 (A). H. oubatchensis Schlechter. New Caledonia: McKee 3306 (A). H. pachyrhiza Steud. Australia: C. L. Wilson 861 (US). H. pancheri (Porch. & Seb.) Briq. New Caledonia: Thorne 28585 (RSA). H. patula Guillaum. New Caledonia: H. S. McKee 3543 (A). H. procumbens DC. Australia: Long 209 (A). H. pulchella Schlechter. New Caledonia: H. S. McKee 2381 (A). H. pungens Benth. Australia: Royce 7640 (PERTH). H. quadricolor Domin. Australia: C. L. Wilson 853 (US). H. racemosa (Endl.) Gilg. Australia: C. L. Wilson 811 (US). H. rhadinopoda F. Muell. Australia: Pritzel 97 (A). H. salicifolia F. Muell, Australia: Queensland. C. L. Wilson 625 (US). H. saligna R.Br. ex DC. Australia: New South Wales. Constable 43107 (NSW). H. scabra Brongn. & Gris. New Caledonia: Thorne 28545 (RSA).

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H. scandens (Willd.) Dryand. Australia: Cult. BRI, s.n. (preserved material); Cult. K, s.n. (preserved material). H. sericea (R.Br.) Benth. Australia: Muir 855 (A). H. serrata Hotchkiss. Australia: C. L. Wilson 855 (US). H. stirlingii C. T. White. Australia: C. L. Wilson 757 (US). H. stricta (DC.) R.Br. ex F. Muell. Australia: Hoogland 8420 (CANB). H. subvaginata (Steud.) Ostenf. Australia: C. L. Wilson 764 (US). H. tetrandra (Lindl.) Gilg. Australia: C. L. Wilson 848 (US); Cult. K, s.n. (preserved material); Cult. E, C3544. H. tomentosa R.Br. Australia: Specht 638 (A). H. tontoutensia Guillaum. New Caledonia: McMillan 5060 (A). H. trachyphylla Schlechter. New Caledonia: Hürlimann 846 (A). H. uncinata (Benth.) F. Muell. Australia: E. H. Wilson 155 (A). H. vaginata (Benth.) F. Muell. Australia: C. L. Wilson 859 (US). H. vestita A. Cunn. Australia: New South Wales. NSW 55998 (A). H. wagapii Gilg. New Caledonia: Thorne 28266 (GH).

Pachynema dilatatum Benth. Australia: Northern Territory. NT 6129. P. junceum Benth. Australia: Northern Territory. NT 6750.

Schumacheria castaneifolia Vahl. Ceylon: Abeywickrama s.n. (preserved material). S. angustifolia Hook. f. & Thoms. Ceylon: US 597415.

Tetracera akara (Burm. f.) Merr. Borneo: Elmer 21314 (A). T. arborescens Jack. Sumatra: Toroes 5293 (A). T. asiatica (Lour.) Hoogl. Hainan: Lau 3875 (A). T. asiatica (Lour.) Hoogl. ssp. asiatica Hoogl. China: Liang 69507 (A). T. boiviniana Baill. Tanganyika: Tanner 2548 (UC). T. daemeliana F. Muell. Australia: C. T. White 11690 (A). T. euryandra Vahl. New Caledonia: Taylor 2 (A). T. indica (Houtt. ex Christm. & Panz.) Merr. Singapore: H. Keng s.n. (preserved material). T. korthalsii Miq. var. subrotunda (Elm.) Hoogl. Borneo: Elmer 21376 (GH). T. leiocarpa Stapf. Liberia: Cooper 45 (GH). T. macrophylla Wall. ex Hook. f. & Thoms. Singapore: Canright 1127 (ASU). T. masuiana De Wild. & Th. Dur. Congo: Becquaert 37 (GH). T. nordtiana F. Muell. var. nordtiana. New Guinea: L. J. Brass 7480 (A). T. ovalifolia DC. Panama: Johnston 1140 (GH); Brazil: Dusén 14630 (MO). T. portobellensis Buerling. Bolivia: Steinbach 7229 (MO). T. scandens (L.) Merr. Philippines: Lagrimas s.n. (preserved material). T. volubilis L. Mexico: Purpus 7647 (MO).

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DEPARTMENT OF BIOLOGY VIRGINIA POLYTECHNIC INSTITUTE BLACKSBURG, VIRGINIA 24061

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EXPLANATION OF PLATES

PLATE I

FIGS. 1-8. Dilleniaceae, nodal anatomy. 1, Tetracera indica (seed received from H. Keng, Singapore), transverse section of cotyledonary node showing unilacunar two-trace condition (c.t., cotyledonary trace), \times 32. 2, Hibbertia pungens (Royce 7640), transverse section of unilacunar node, \times 32. 3, Tetracera boiviniana (Tanner 2548), transverse section of trilacunar node illustrating widely separated gaps, \times 13. 4, Acrotrema sp. (Thwaites CP3899), transverse section through rhizome in region of leaf trace (lt) and adventitious root departure, \times 13. 5, Hibbertia scandens (cult. BRI, s.n.), transverse section of node illustrating trilacunar condition with widely separated gaps and sheathing petiole, \times 13. 6, Davilla rugosa (de Mattos Filho s.n.), tranverse section of pentalacunar node, \times 13. 7, Schumacheria castaneifolia (Abeywickrama s.n.), transverse section of multilacunar node. Note the median trace departs before laterals (lt, leaf trace), \times 13. 8, Dillenia ovata (cult. sing, s.n.), transverse section of multilacunar node illustrating simultaneous departure of leaf traces, X 13.

PLATE II

FIGS. 9, 10. Dilleniaceae, petiolar anatomy. 9A, B, C, D, Acrotrema (Thwaites CP3899), transverse sections of the petiole and midrib illustrating derivation of abaxial arc and adaxial bundle, \times 32. 10A, B, C, Curatella americana (Irwin 5470), transverse sections of petiole illustrating formation of medullary bundles, X 13. 10D, the same, transverse section of petiole at base of lamina showing medullary bundles (indicated by arrows), complete fusion of vascular cylinder, and extraxylary fibers, \times 30.

PLATE III

FIGS. 11–14. Dilleniaceae, petiolar and nodal anatomy. All figures \times 30. 11A, B, C, Hibbertia scandens (cult. BRI, s.n.), transverse sections of petiole illustrating origin of abaxial arc and adaxial bundle. 12, H. dentata (seedling grown from K seed 2264), transverse section of cotyledonary node showing a single broad trace departing the vascular cylinder. 13, H. lucida (C. T. White 2210), transverse section of petiole at base of lamina showing formation of medullary bundles by invagination. 14, H. patula (McKee 3543), transverse section of petiole at base of lamina depicting confluent vascular cylinder. Note sclerotic nature of pith and well developed extraxylary fibers.

PLATE IV

FIGS. 15-22. Dilleniaceae, petiolar anatomy. 15, Didesmandra aspera (Sarawak, s.n.), transverse section of petiole at base of lamina showing widely dissected vascular cylinder, \times 15. 16, Tetracera daemeliana (C. T. White 11690), transverse section of petiole at base of lamina showing flattened, slightly dissected vascular cylinder, \times 32. 17, Hibbertia coriacea (Humbert 5866), transverse section of petiole at base of lamina showing arc of vascular tissue, \times 32. 18, Dillenia castaneifolia (Womersley NGF 3768), transverse section of petiole at base of lamina showing arc of medullary bundles, \times 15. 19, D. bolsteri

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(Wenzel 3112), transverse section of petiole at base of lamina showing confluent "V" shaped vascular cylinder, \times 32. 20, D. beccariana (SAR 16272), transverse section of petiole at base of lamina showing superimposed medullary bundles (indicated by arrows), \times 17. 21, Doliocarpus guianensis (uc 947180), transverse section at base of petiole showing abaxial arc of dissected bundles and adaxial siphonostele, \times 17. 22, Davilla aspera (Howard 10502), transverse section of petiole at base of lamina showing nearly complete vascular cylinder. Note abundant sclereids in cortex, \times 32.

PLATE V

FIGS. 23-26. Dilleniaceae, minor venation. All figures \times 25. 23, Dillenia megalantha (M. Q. Lagrimas s.n.), note prominent parenchymatous bundle sheath and numerous free vein endings. 24, D. papuana (Womersley NGF 3926), note almost complete absence of free vein endings. 25, D. schlechteri (Womersley & Millar NGF 7000), note complete absence of free vein endings accompanied by massive venation and bundle sheathing. Sheath cells extend into vein islets. 26, Didesmandra aspera (SAR S.18297), note weak, slender venation and incomplete bundle sheathing.

PLATE VI

FIGS. 27-30. Dilleniaceae, minor venation. 27, Hibbertia exutiacies (Eichler 17965), base of leaf showing single leaf trace and termination of reflexed lateral veins, \times 35. 28, H. subvaginata (C. L. Wilson 764), note massive venation lacking bundle sheathing, \times 35. 29, H. banksii (Brass 8431), venation showing characteristic interrupted sclerotized sheathing, X 25. 30, H. wagapii (Thorne 28266), note terminal veinlets are completely enclosed by sclerenchymatous bundle sheathing, $\times 25$.

PLATE VII

FIGS. 31-34. Dilleniaceae, minor venation. 31, Curatella americana (Irwin 5470), minor venation showing abundant parenchymatous bundle sheathing, X25. 32, Tetracera macrophylla (Canright 1127), note sclerenchymatous bundle sheathing completely surrounds terminal tracheids, \times 25. 33, Doliocarpus dentatus (Krukoff 10088), terminal veinlet with abundant parenchymatous sheathing. Note sheath cells often orientated at right angles to vein, \times 54. 34, Pachynema dilatatum (NT 6129), scale-like leaf vascularized by weak cauline traces, \times 54.

PLATE VIII

FIGS. 35-39. Terminal veinlet idioblasts in Hibbertia. 35, H. scandens (cult. к, s.n.), X 130. 36, H. dentata (cult. к, s.n.), X 120. 37, H. huegelli (C. L. Wilson 777), X 100. 38, H. pachyrhiza (C. L. Wilson 861), X 130. 39, H. scandens (cult. K, s.n.), X 120.

PLATE IX

FIGS. 40-44. Dilleniaceae, major venation. 40, Dillenia indica (seed received from H. Keng, Singapore), cotyledonary node and vascularization of cotyledon. 41, the same, vascularization of first foliage node and leaf. 42, Hibbertia dentata (cult. K, s.n.), natural size. 43, H. tontoutensia (McMillan 5060), \times 1.2. 44, H. cuneiformis (Wilson 297), $\times 2.5$.

PLATE X

FIGS. 45-50. Leaf vascularization in Hibbertia. Due to fluctuations in leaf size, magnifications given are intended to indicate only general size ranges. 45, H. huegelli (C. L. Wilson 777), \times 3.5. 46, H. monogyna (Maiden s.n.), \times 4. 47, H. nitida (Fl. Novae Holl. 141), X 5. 48, H. vestita (NSW 55998), X 13. 49, H. exutiacies (Eichler 17965), X 9. 50, H. fasciculata (Aston 387), X 9.

PLATE I



PLATE II



PLATE III



PLATE IV



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PLATE V

PLATE VI

PLATE VII

PLATE VIII

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PLATE IX

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ANATOMY AND ONTOGENY OF THE CINCINNI AND FLOWERS IN NANNORRHOPS RITCHIANA (PALMAE) ¹

NATALIE W. UHL

THE LARGE, TERMINAL, compound inflorescence of Nannorrhops ritchiana

(Palmae-Coryphoideae) is composed of unspecialized branch systems (Tomlinson & Moore, 1968) which may serve as a model for the derivation of more specialized types of palm inflorescence. Observations on the inflorescence of *Nannorrhops ritchiana* are continued here with a description of the anatomy and some aspects of the ontogeny of the rachillae, of the ultimate flowering units, and of the flowers. *Nannorrhops* is especially important because completely sheathing and vasculated bracteoles are present throughout the ultimate flowering unit. Detailed studies confirm Tomlinson and Moore's tentative designation of this unit as a cincinnus and reveal basic constructional principles that apply to many, if not all, of the varied flowering units found in palms; e.g. the triad of a pistillate and two staminate flowers, where interpretation has been difficult because bracts are absent or lack vasculature (Uhl, 1966). The form and anatomy of the carpel may also illustrate some primitive features for palms.

MATERIAL AND METHODS

Inflorescence branches from plants at the Fairchild Tropical Garden, Miami, Florida, were available in various stages of development from the following collections: *Moore 6009*, *Read 735*, and *Tomlinson* 14.XI.63 and 14.XI.66. These were fixed in formalin-acetic acid-ethanol, desilicified for 1 to 2 weeks with approximately 1/3 commercial strength hydrofluoric acid, and embedded in Paraplast. Serial sections of flowers and rachillae were made at 5, 7, 10, and 15 microns and were stained with safranin and fast green or safranin and aniline blue. Cincinni and flowers were also cleared as described previously (Uhl, 1966), the number of cleared flowers examined exceeding 50. Two films were prepared for cinematographic analysis (Tomlinson & Zimmermann, 1965) of rachillae and mature flowers. Some observations and photographs (FIGS. 8–19) were made in polarized light. Since growth is continuous, but not uniform, dimensions of the ma-

terial examined are included below.

RACHILLAE

Morphology. Structural patterns are simple despite the large size of the inflorescence in Nannorrhops (Tomlinson & Moore, 1968, Fig. 42). Up ¹From work supported by National Science Foundation Grant GB-7758; principal investigator, Harold E. Moore, Jr.

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to five orders of branches are formed monopodially. The visible flowerbearing axes or rachillae are mostly branches of the fourth order, but whatever the order, they are similar in size and in the number of flowerclusters or cincinni produced. Rachillae taper slightly in diameter (from 1.5 mm. to 0.75 mm.) and are indeterminate in length and in potential number of flower clusters. Fully expanded rachillae in the material examined range from 5 to 12 cm. in length and bear from about 20 to 45 cincinni. A few distal cincinni are usually abortive.

Development. Maturation of flowering axes within the inflorescence is complex. Four different patterns can be recognized: one with reference to the inflorescence as a whole, a second in the sequence of development of lateral branches, a third on individual rachillae, and a fourth within each flower cluster.

FIGS. 1-7. FIGS. 1-3, Three successive developmental stages of a third order branch, arrows indicate sequence, further explanation in text. FIG. 1, immature third order branch, \times 1.5; FIG. 2, third order branch, later stage than FIG. 1, some fourth order branches much larger than others, \times 1.5; FIG. 3, third order branch (bracketed) on second order branch, subtending bract removed, \times 0.5; FIG. 4, a cincinnus, flowers in bud, all bracts removed, \times 6; FIG. 5, open flowers, upper with one petal and one stamen removed, \times 5; FIG. 6, part of a cleared rachilla to show bundles in bracts subtending stalks of first flowers of cincinni, \times 4; FIG. 7, central part of a cleared flower to show vascular system and five bundles in stalk, arrow indicates large, fused bundles opposite sepal insertion. DETAILS: fb, fibrous bundle in bract; fl s, stalk of first flower of a cincinnus; mv, midvein of the bract; pe, petal (removed); se, sepal tube; st, stamen (removed).